

Multi-species Mating Swarms of *Formica* in Southwestern Montana, U.S.A. (Hymenoptera: Formicidae)

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Abstract.—In 1995 and 1996 in southwestern Montana, I observed ant mating swarms that each day consisted of at least two of three species of *Formica*: *Formica ciliata* Mayr, *Formica obtusopilosa* Emery, and *Formica subpolita* Mayr. In 1993, *F. ciliata* males also formed swarms above the nest from which they emerged. Although swarming behaviors of males of these species were indistinguishable, the mating posture, the behavior of females during mating, and the duration of mating varied among species. *Formica ciliata* matings averaged five times longer than *F. obtusopilosa* matings and four times longer than *F. subpolita* matings. Predation on alate males at swarms was frequent, with the spider *Dictyna coloradensis* (Dictynidae) probably accounting for most mortality.

The study of ant mating strategies is not only a tool for examining standard aspects of sexual selection theory (e.g. sperm competition), but is critical to an understanding of the social behavior of ants (Bourke and Franks 1995). It is becoming clear that ant mating systems and social systems may have reciprocal influences upon one another. For example, on the one hand, the number of times that a queen mates determines the relatedness among her offspring, which influences the evolution of eusocial behavior (Crozier and Pamilo 1996). On the other hand, intracolony relatedness (along with possible detriments to inbreeding) determines the cost of mating with another colony member, and thus may influence which mating system reduces the risk of inbreeding (Ross and Keller 1995). Although progress is being made in answering these important questions (e.g. Keller and Passera 1993), we still need to learn much more about the basic form of mating systems in the Formicidae (Hölldobler and Wilson 1990).

Perhaps the most common mating system in ants is for alates to congregate and mate within short-lived swarms (Bourke and Franks 1995). Although swarms often

consist of a single species of ant, multi-species swarms have also been reported (Chapman 1954, 1963, Collingwood 1958, LePrince and Francoeur 1986). In a previous paper, I noted that alates of three unidentified species of *Formica* were occasionally present in small numbers within swarms of *Formica subpolita* at one location in southwestern Montana, U.S.A. (O'Neill 1994). Here, I report on *Formica* mating swarms at nearby location which often consisted of mixtures of swarming males and mating pairs of three species, *Formica ciliata*, *F. obtusopilosa*, and *F. subpolita*. I also provide comparative information on the mating behavior of the three species and data on the high level of predation on alates within swarms.

METHODS

I observed the ants at a site 2 km NW of Logan, Gallatin Co., MT, U.S.A. (45°45'N, 111°35'W) in July of 1993, 1995, and 1996. I visited the site on 18 days, to check for swarms, which were present on 8 days; on five days in 1996, I was present for the entire swarm period. I collected 53 mating pairs for later identification. Females of the three species were easy to

identify in the field, *Formica ciliata* females being completely orange, *F. obtusopilosa* females having orange thoraces, but black heads and abdomens, and *F. subpolita* females being completely shiny black and larger than queens of the other two species. It was much more difficult to identify males in the field. However, once I associated males with females in mating pairs a suite of characters associated with each species and species group (Wheeler and Wheeler 1963) allowed reliable identification of males in the lab; voucher specimens of males and females from mating pairs of all three species have been deposited in the Montana State University Entomology Collection. On six days in 1995 and 1996, I collected alates from spider webs, feeding spiders, or other arthropod predators. All prey were collected within the area encompassed by swarms, during swarming or immediately afterwards.

RESULTS

Swarm Location.—I observed *Formica* mating swarms at two locations. In 1993, a swarm of *F. ciliata* was present on 19 and 20 July just above a large, multi-entrance *F. ciliata* nest on the west side of a grassy ridge among scattered junipers (*Juniperus scopulorum* Sarg.) and yucca (*Yucca glauca* Nutt.). The swarms, which at their peak covered about 2×10 m and probably included >200 males, were centered around a patch of yellow sweetclover (*Melilotus officinalis* L.) growing among the nest entrances. Swarms did not form above the nest in 1995 and 1996. Although many alate male and female *F. ciliata* emerged from the colony, they climbed nearby plants and flew away, perhaps to join swarms that I found on a hillside approximately 100 m east of the *F. ciliata* nest. Swarms at this second location were concentrated on the lower half of the hillside, where it was covered by a dense expanse of cheatgrass (*Bromus tectorum* L.) and several clusters of dead and leafless yellow

sweetclover. Swarms were sometimes restricted to several square meters, but at times certainly consisted of over 500 males swarming over an area of $\sim 5 \times 50$ m (with highly variable density across the swarm). Because I found no *Formica* nests with emerging alates within the swarm area, the alates probably originated elsewhere.

Species Composition of Swarms.—Unlike the swarms above the *F. ciliata* nest, those on the hillside always contained males and females of two or three species: *F. ciliata*, *F. obtusopilosa*, and *F. subpolita*. The exact mix of species within swarms was hard to determine because males were difficult to identify and count in the field. However, by identifying females in mating pairs I was able to determine that at least two species were present on each of six days in 1996 (Fig. 1). The relative number of matings observed, however, cannot be used to estimate the relative number of swarming males. Because matings of *F. ciliata* lasted much longer than those of the other two species (see below), the probability of encountering a pair of *F. ciliata* was much higher. It was my impression, however, that *F. subpolita* males were most common, whereas those of *F. obtusopilosa* were least common. This was confirmed by examining males in webs of the spider *Dictyna coloradensis* (see below), which were situated at swarm height and probably captured a representative sample of swarming males. Of the 292 alate males I recovered from *Dictyna* webs, 70.5% were *F. subpolita*, 25.7% were *F. ciliata*, 2.1% were *F. obtusopilosa*, and 1.7% were of one or more other species of *Formica* that apparently joined swarms on occasion. I also found one female each of two unidentified *Formica* perched on plants in the swarm area.

While swarms were in progress, females of the three *Formica* species often perched within 1 m of one another. The overlapping spatial distribution of the females suggests that swarming males of the three

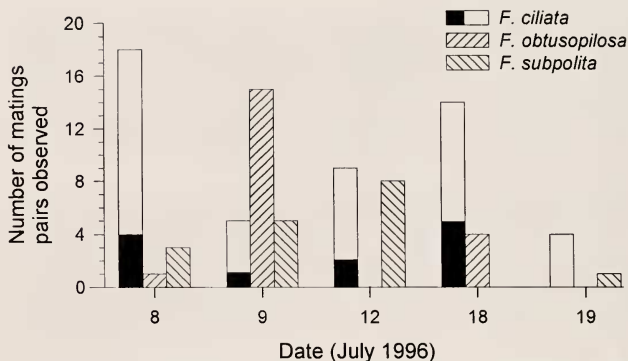


Fig. 1. The number of mating pairs of three species observed at the hillside site on the five days in 1996 when observers were present during the entire swarm period (solid black portions of the *F. ciliata* bars indicate those matings that were the 2nd, 3rd, or 4th for an individual female; no multiple matings were observed for *F. obtusopilosa* on these days, and multiple matings were not recorded for *F. subpolita* in this study).

species also intermingled. Nevertheless, on several days there was a larger scale, though incomplete, segregation of the species at the hillside site. Female *F. ciliata* tended perch in the center and in the northern end of the elongate swarm, while female *F. subpolita* were most abundant at either end of the swarm. The female *F. obtusopilosa* were generally restricted to a small area in the northern half of the swarm. There was also interspecific variation in activity periods. At the hillside site, swarms were active between 0900 and 1130 h on warm, clear days. As judged by the times at which I observed matings in 1996, *F. ciliata* also had a longer daily mating period than the other two species which displayed a more prominent peak of mating activity around 1000 h (Fig. 2).

Swarming and Mating Behavior.—Only males actually swarmed, whereas females perched on low vegetation. Swarming behavior of male *F. ciliata* and *F. obtusopilosa* was similar to that previously described

for *F. subpolita* (O'Neill 1994). Males of all three species made slow, irregular flights near the top of the vegetation, generally facing into the wind. Males often restricted their flights to the immediate vicinity of a perched female, eventually landing on the plant and walking along its stems. When a male approached the female, usually after exploring several stems, his body and wings vibrated rapidly, perhaps responding to olfactory cues emanating from the female (Cherix et al. 1993). This behavior near females has also been noted for other species of *Formica* (Kannowski and Johnson 1969, Henderson and Jeanne 1992).

O'Neill (1994) provided descriptions of matings of *F. subpolita*, which typically proceeded as follows. A male mounted a female dorsally, facing the same direction as her, and immediately coupled if she acquiesced. He then released his grip and flipped backwards 180° so that he now faced the opposite direction, venter up. After an average of 27 s (range: 4–63), the

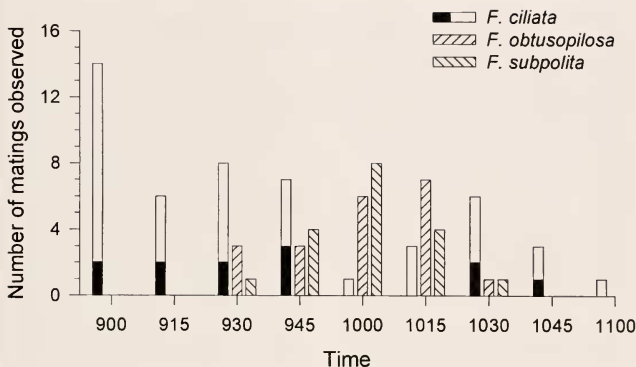


Fig. 2. The frequency distribution of matings observed in 15-min intervals (beginning at the time indicated) on the same five days depicted in Fig. 1 (see Fig. 1 for note on occurrence of multiple matings).

female usually curled her body back and began biting the male, often on the petiole. Nevertheless, mating continued for another 35 s on average, so that complete matings averaged 62 s (range: 28 to 94). Overall, matings of *F. obtusopilosa* were similar to those of *F. subpolita*, although the mean time to biting was just 16.3 s (SE = 2.5; N = 13; range: 2 to 33) and the total duration of mating was 50.6 s (SE = 6.7; N = 13). Biting by females occurred in all 13 *F. obtusopilosa* matings observed from start to finish, whereas it occurred in 88% of *F. subpolita* matings (O'Neill 1994).

Mating by *F. ciliata* was initiated in the same manner as in *F. subpolita* and *F. obtusopilosa*, but it was different in form and duration. After a male *F. ciliata* released his leg grip on the female, he remained arched forward, so that his head was positioned above the female's abdomen. Furthermore, during the prolonged matings, which averaged 260.1 ± 22.0 s (range: 7 to 711 s; N = 54), females rarely reached back to bite males (6% of 54 matings). Thus, the form and duration of mating ap-

pears to be relatively species-specific. However, during *Formica obscuripes* Forel matings, males apparently could adopt either of the postures observed in my study (Talbot 1972).

During mating, one or two other males sometimes arrived and attempted coupling, apparently oblivious to the presence of the copulating male. Twice, a second *F. ciliata* male arrived soon after a mating commenced and disrupted the mating pair. However, neither intruding male was able to mate with the female. These interactions probably resulted when males incidentally homed to the same female, and apparently do not represent fighting for possession of receptive females.

Following mating, females of all three species either left the swarm area by flying upwards or they remained on the same plant awaiting the arrival of another male. Polyandry is a common feature of ant mating systems, especially in the genus *Formica*, where the existence of multiple mating by females has been observed or inferred in 15 of 16 species cited by Cro-

zier and Pamilo (1996). One of these species is *F. subpolita*, whose females mate up to four times each within mating swarms (O'Neill 1994). By continuing to watch females from the time they were first observed in copula until they left the area, I also confirmed that polyandry occurs in *F. obtusopilosa* and *F. ciliata*. One female *F. obtusopilosa* was seen to mate three times. Eleven *F. ciliata* females were seen to mate twice, three mated three times, and one mated four times. Not all females were observed continuously, some were collected, and some may have mated prior to my first observation. Thus, multiple mating in these species is probably more common, and each female probably mates more frequently than my observations suggest. The multiple matings by a single *F. ciliata* female typically occurred over a limited portion of the daily swarm period. The mean interval between the termination of one mating and initiation of the next was 5.3 min (SE = 0.9, N = 12), and one *F. ciliata* female mated four times within 31.1 min.

Although females and males of the three species were in close proximity, I found no evidence of cross-species matings among the 53 mating pairs collected and examined. It is possible that males attempted to mate with females of other species, because I observed rejection of "courting" males by females of all three species; unreceptive *Formica* females rejected mating attempts by curling the tips of their abdomens away from mounted males, by walking away, or by dropping off the plant. In all three species, rejections occurred most often just before a female flew away from the swarm, so perhaps the rejections usually signal the end of the receptivity to conspecific males. On several occasions, females remained on their perches after rejecting one male, and soon mated with another. These rejections could represent intraspecific female choice, or females rejecting courting males of other species, but because none of these

rejected males were collected, I could not ascertain their identity.

Predation on Alates.—Predations on alates, particularly by spiders and robber flies were common at the hillside site (Table 1). There are three apparent reasons why males made up 98% of the prey. First, males probably far outnumbered females at any given time. Second, because males spent much of the time in flight above the vegetation, they were more susceptible to predation by visually hunting robber flies that intercept airborne prey within swarms (O'Neill 1992). Third, the most common spiders, *D. coloradensis*, built their webs at the tips of plant stems, where single webs captured up to eight males on a single day. Because males flew at the same height as the webs and explored the stems of many plants during a day, they increased their likelihood of contacting a web.

DISCUSSION

The mating systems of *F. ciliata*, *F. obtusopilosa*, and *F. subpolita* exhibit features in common with many species of ants, including male swarming, a lack of overt fighting among males, and multiple mating by females (Bourke and Franks 1994). Although swarming is common in *Formica*, the locations of swarms relative to the nests from which alates emerge vary both within and between species. Swarming and pairing at variable or unknown distances from nests have been seen for *Formica lugubris* Zett. (Cherix et al. 1993), *Formica obscuripes* Forel (Talbot 1959, 1972), *Formica subnuda* Emery (Chapman 1954, 1963), and *F. subpolita* (O'Neill 1994). Swarming at nests from which the alates emerged has been observed in *Formica dakotensis* Emery (Talbot 1971) and *Formica montana* Emery (Kannowski and Johnson 1969, Henderson and Jeanne 1992). Although many female *Formica pergandei* Emery mate within swarms at their home nests, some apparently disperse prior to mating, presumably to enter swarms else-

Table 1. Arthropods observed capturing or feeding on alate ants at mating swarms. The category "Formica spp." includes members of the other three species that were not identified in the field.

Predator	Prey species and sex			
	<i>F. ciliata</i>	<i>F. obtusopilosa</i>	<i>F. subpolita</i>	<i>Formica</i> spp.
ARACHNIDA				
Araneidae				
<i>Metepeira foxi</i> Gerstch and Ivie	1 m	—	1 m	—
unidentified araneid	—	—	15 m	—
Dictynidae				
<i>Dictyna coloradensis</i> Chamberlin	75 m	6 m	206 m, 1 f	5 m
Philodromidae				
<i>Tibellus duttoni</i> (Hentz)	—	—	2 m	—
Thomisidae				
<i>Misumenops celer</i> (Hentz)	1 m	—	—	—
ORTHOPTERA				
Acrididae				
<i>Melanoplus sanguinipes</i> (Fabricius)	—	—	—	3 m ¹
HEMIPTERA				
Nabidae				
unidentified nymphs	2 m	—	—	—
Reduviidae				
unidentified nymphs	1 m	—	—	—
DIPTERA				
Asilidae				
<i>Efferia staminea</i> (Williston)	1 f	—	—	22 m
<i>Megaphorus willistoni</i> (Cole)	—	—	1 f	19 m
<i>Stenopogon inquinatus</i> (Loew)	—	—	—	2 m
HYMENOPTERA				
Sphecidae				
<i>Aphilanthops subfrigidus</i>	1 f	—	3 f	—

¹ All 5th instars which did not prey on the ants, but rather scavenged them from webs of *D. coloradensis*.

where (Kannowski and Johnson 1969). In southwest Montana, *F. ciliata* swarmed both above nests (in 1993) and within multi-species swarms in a area apparently not harboring any *F. ciliata* nests (in 1995 and 1996). Alates of *F. obtusopilosa* and *F. subpolita* also apparently originated from colonies outside of the swarm area.

There are several potential advantages to be gained by alates that join swarms away from their home nests. First, when colonies produce reproductives of just one sex, the alates from some nests must disperse in order to find mates. For example,

because many *F. montana* colonies produce only male alates, they must disperse and swarm at nests that have produced females (Henderson and Jeanne 1992). Because I saw both male and female alates emerging from the *F. ciliata* colony in 1995 and 1996 when swarms occurred away from the nest, alates of this species appear to have dispersed for other reasons. Second, if extreme inbreeding is detrimental, alates that join multi-colony swarms away from the home nest, will be more likely to mate with non-relatives. Inbreeding would be more likely in monogynous

nesses, since many of the alates would be full siblings. Comparative evidence suggests that alate queens from monogynous nests tend to join swarms at a great distance away, but that females from polygynous colonies (which are presumably more genetically diverse) disperse much shorter distances, sometimes mating on or within the nest (Ross and Keller 1995). I cannot directly address this hypothesis as it applies to *F. ciliata*, *F. obtusopilosa*, and *F. subpolita*, because I do not know whether queens within swarms came from monogynous or polygynous colonies. Joining large multi-colony swarms could reduce the risk inbreeding, but when swarms include more than one species, there is the added problem of identifying potential mates of the correct species. This problem could perhaps be solved if the sex pheromones released by females (Cherix et al. 1993) provided species-specificity.

Formica ciliata, *F. obtusopilosa*, and *F. subpolita* not only swarm away from their home nests, but gather together in various combinations at the same location on at least two successive years; at a nearby site, *F. subpolita* swarms were observed in the same location on six consecutive years (O'Neill 1994). Multi-species mating swarms also occur in other species of ants, and sometimes involve species of different genera (Chapman 1954, 1963, Collingwood 1958, Leprince and Francoeur 1986). Perhaps different species of ants swarm at the same times and places because alates of each species coincidentally respond to the same habitat cues. However, there may be an advantage to joining high density multispecies swarms if individual alates reduce their risk of predation when predators become temporarily satiated by the glut of food (Hölldobler and Wilson 1990, Bourke and Franks 1995); because at least some colonies would have to join multispecies swarms away from their home nests, this would also promote mating away from nests. Ant mating swarms often provide a flush of prey for a variety

of predators (Whitcomb et al. 1973, Robertson and Villet 1989, O'Neill 1990, 1992, 1994) that may impose a substantial cost on colonies. It is possible that some of the predators at the hillside site became satiated during swarms, thus temporarily reducing the predation risk of the surviving males. O'Neill (1992) found that, during the peak of *F. subpolita* swarms, the great majority of robber flies (primarily *Efferia staminea*) were feeding. When swarms were absent, most of these robber flies were not feeding (although they were actively foraging). However, it seems unlikely that the web building spiders become effectively satiated, because males continued to be trapped in webs throughout a swarm period and full webs were never observed. Finally, it should be noted that the satiation effect might be offset if predators congregated in areas of high prey density, thus actually increasing the risk of predation at swarm sites.

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